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INSTINCT, ESPECIALLY IN SOLITARY WASPS.

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I. THE PLACE OF INSTINCT IN ANIMAL DEVELOPMENT.

§ 1. IN a recent number of the *British Journal of Psychology*, the relations between Instinct and Intelligence were fully discussed and illustrated in various aspects by several distinguished writers. There was general agreement that these functions are not opposed one to another in any exclusive way but co-operate in the life of animals. This is so plain to anyone who considers the facts that we wonder how other views should still so widely prevail. The popular belief, shared by some scientific men, seems to depend upon three influences: (1) the doctrine of special creation, according to which each kind of animal has its own endowment of instincts, infallible, invariable, and universally present in the individuals of each kind; (2) the Cartesian doctrine that every animal is a machine, whilst man alone is intelligent; (3) Spencer's theory of the development in animals of adjustment to external relations from irritability and contractility in zoophytes, simple reflex action in creatures that are first found with distinct tissues of nerves and muscles, through compound reflexes to instincts, in which consciousness first appears, and finally intelligence when instinct breaks down because the increasing complexity of the conditions which an organism has to deal with can only be met by a hesitating reaction. Romanes criticised Spencer's theory effectively at many points; maintaining that instinct and intelligence are not successive manifestations of conscious life; but that, while "secondary instincts" are due to inherited habits and "lapsed intelligence" (Lewes), and therefore later than intelligence, the greater number of instincts, the "primary" on the one hand, and intelligence on the other, are, by natural selection, differentiated from the common ground of perception. He did not, however, realise how early the signs of consciousness and intelligence are manifested in animal life, and the doctrine of inherited habits has become unpopular amongst Biologists.

Even popular observation knows that instincts are not infallible, that birds sometimes fail to migrate in time, that the hosts of a cuckoo cannot distinguish the parasite's egg or fledgling from their own, that cattle sometimes devour poisonous herbs, and so on; and it is plain that, if animals had once been infallibly endowed, nothing but a perpetual miracle could have kept them adapted to the ever-changing conditions of their habitat. The variability of instincts, as in the nesting of birds, is also in fact popularly known; and if they were not variable, their origin could never be explained. That instincts and all animal activities may be explained by comparing an animal with a machine has a certain value by way of generalisation; and it is better than any hypothesis of vitalism, that merely gives a general name to the activities of living things without explaining any of them; but as the notion of mechanism takes no account of all the *propria* of living things in which they differ from machines, it can only stand in the background as a type of the precision and rigour of causal explanation that is to be sought for in Biology[1].

[1] See the discussion of this matter by H. S. Jennings in the *American Journ. of Psych.*, July, 1910.

The "universality" of instinct amongst animals may be understood in two ways. First it may mean that every individual of any species exhibits the same instincts, if not always in the same perfection. But this is not true wherever dimorphism appears, whether sexually or in the more special forms that are found in ants and termites; since each sex- or "caste-" form (soldier or worker) has its own instincts. But the "universality" of instinct may be understood in another way, namely that instinctive action is found throughout the animal kingdom (except in man), or even that it is the sole adaptive function of animals. But when we spread out the facts before us three observations are almost unavoidable. The first is that the order of development indicated by Spencer—irritability, reflex action, compound reflex action, instinct—has some validity. It seems at least highly convenient to confine the term instinct to certain complex modes of reaction which have in general the aspect of compound reflexes, but may be distinguished from other compound reflexes by involving the adjustment—apparently the attentive adjustment—of the animal as a whole, and thereby exhibiting what has been called "behaviour" (Lloyd Morgan). [Other differences will be mentioned below.] But then innumerable animals below the Coelenterata, having no nervous system, and therefore no reflex action, and incapable of what we call instinct, nevertheless exhibit behaviour—adjustment of the animal as a whole. To describe it as irritability and contractility gives no adequate impression of the unity of their life. Their activities have been aptly termed "tropisms," being in close analogy with the reactions of plants to light, contact, gravity; and how high such reactions can rise without a nervous system may be read in many passages of Darwin's botanical writings. On the other hand, when we look at the higher levels of vertebrate life, especially amongst monkeys, we see that their behaviour rarely exhibits the regularity and predictability that are usually considered to be appropriate marks of instinct.

The second observation which on a fair view of the facts we can hardly help making is, that the behaviour of even the simplest animals, exhibiting only tropisms, is not entirely predictable; does not depend merely upon stimuli; but also upon each animal's internal condition; and moreover that it shows plasticity, reactions to stimuli that are not prearranged, "fatal" adjustments, but in the nature of trials; and finally that their behaviour is not without intelligence, but evinces (*a*) discrimination and recognition by pursuit and avoidance, and (*b*) memory, or learning by the experience that results from its trial-movements.

My third observation is that the tropisms and intelligence that appear in the earliest forms of life never afterwards disappear. For we cannot suppose with Spencer and Romanes that consciousness is first found at some stage in the development of animals, as a result of the complexity of organisation, hesitancy or delay of reaction, seeing that the signs of consciousness are present in the simplest; nor do we find that discrimination and memory are at any stage lost, to be afterwards recovered. There is, no doubt, opposition between the complete organisation of a reflex arc, and the manifestation of intelligence; and we are apt to assume that the whole life of a lowly organism is similar to the more completely integrated structures of our own bodies, which seem to us unconscious. But this is a very disputable analogy; for in complex organisms with division of labour the lead in adaptive variation is restricted to special organs. As intelligence persists, so also do the tropisms at all stages of development; originally independent of a nervous system, they are taken up by such systems as soon as these are formed, and extensively influence the conduct of all animals, including ourselves. I am inclined to believe that the explanation of every instinct will lead us back to a tropism or tropisms.

§ 2. Instinct, then, is a name for certain complex functions that help to maintain the life of animals at certain stages of development, but at earlier stages do not yet exist, and at the latest stages are superseded, or rather so modified by intelligence as to deserve another name—instinctive dispositions. To see the full meaning of this it may be well to distinguish two kinds of instincts: (*a*) the impulsive kind such as pugnacity, flight, gregariousness, which are satisfied each by complex activities of similar quality having one end—to overcome, to escape, to mingle with the herd; and (*b*) chain-instincts, such as migration and spawning, nesting and incubation, etc.; which, though tending to one result, yet advance by a series of diverse actions each of which probably has its own satisfaction. It is of these chain-instincts that solitary wasps present the most astonishing examples. And when we say that instincts fail to develop in the higher vertebrates, it is of the chain-instincts that this is most nearly true. For the impulsive instincts, though normally modified or restrained by an intelligent appreciation of circumstances, yet sometimes, when the stimulus is strong (relatively to the individual) and the conditions of inhibition are weak (or faintly appreciated), display themselves even in civilised men with all the features of brutal incontinence. The chain-instincts everywhere subserve especially the reproduction of the species; and in the higher vertebrates that stage of the instinct which is concerned with the rearing of offspring is carried out with such intelligent variety of adaptations to circumstances that its instinctive character is almost completely disguised. Yet when we consider that the end in nature of all such activities is the ensuring of future generations, it becomes plain that no animal can understand this, and that therefore the activities remain essentially instinctive until some pretty late condition of savage humanity; and even then perhaps may be possible for "intelligence," not by a representation of the end in nature, but only through an idea of the necessity of having successors to perform one's funerary rites; for a knowledge of the end can be of no avail if it be not strongly desired. Indeed the desire for posterity in most of us would not stay the world from depopulation without the instinctive affection of mothers.

Whilst, on the one hand, instincts are only masked by intelligent activities (to which they impart all their vigour), on the other hand, they cannot, I believe, be marked off from compound reflexes definitely, but only by considerations of more or less through a series of distinctions. (*a*) Instincts, as we have seen, are connate connections between stimuli and reactions of the organism as a whole; but this definition includes the action of a dog scratching himself, of a child writhing on being tickled; and such actions are usually considered to be compound reflexes. (*b*) Probably instincts are accompanied by the fuller consciousness of some object and cravings aroused by it, of effort and excitement in working themselves out, of satisfaction in the fulfilment; but without much forcing these features may be found in the scratch-reflex. (*c*) In reflex action the purpose served is often immediate, as in blinking to moisten the eye, withdrawing one's hand from a thorn; whereas many instincts have remote ends, as in making a nest, or storing nuts for the winter: yet the instinctive action of lying quite still may have the immediate effect of escaping an enemy; whilst the reflex of swallowing has the remote end of digestion and assimilation: but blinking and swallowing are not actions of the organism as a whole. (*d*) Instincts are the more complex; they often consist of many diverse yet co-ordinated actions, whether in chains like nesting, incubation, etc., or in the miscellaneous distribution of a fight; whereas even a chain-reflex, such as swallowing, consists in the repetition of the same action; or if it be said that swallowing must be taken with the ensuing diverse processes of digestion, still there is nowhere the activity of the whole organism. (*e*) Whilst reflex action is often, instinct is always, concerned with external relations: thus eating is the instinctive beginning which swallowing gives effect to. And it is this concern with external relations, even to remote events, that excites our wonder, because in this it is like reason; whereas the complex internal physiological processes, common to us with the animals and "unconscious" in both, are taken as a matter of course, though no less wonderful. (*f*) Whilst in most animals the reflexes are organised at birth and in none are long deferred, the instincts may not appear until late in life; their action is then a mark of maturity, constitutes a crisis in the animal's life-history, and alters its whole character. (*g*) Moreover, being later acquired than reflexes, the instincts are less strictly organised and more variable or plastic; and it is on this ground that C. S. Myers[1] (as I understand him) regards instinct as expressing a rudimentary intelligence. Of course, I agree with him in supposing all animal activities to have some degree of consciousness. On the whole, if the division between compound reflexes and instincts and intelligence is still indefinite, it is such as we should expect in Biology. Their differences are enough to make the terms intelligible: remembering that in Biology and Psychology we may distinguish but cannot separate, since no function or faculty has independent existence. As there are real resemblances between the meanings of "tropism," "reflex," "instinct," "intelligence," an ingenious man can stretch any one of these words until he seems to make it cover the whole field of animal activity; but in doing so he must efface all differences. The reasonable course is to distribute these, or other suitable words, over the field so as to divide it amongst them in the most convenient way on the whole; that is, according to the most important differences that can be discovered.

§ 3. The prominence or importance of instinct in an animal's life varies greatly from one order or division to another. It seems to reach its greatest development in certain insects and in spiders. Its utility consists in preparing for unforeseen and often remote events: when a spider first spins its web or constructs a trap, it cannot foresee that flies or other insects will fall into it; when a sand-wasp digs its nest it cannot foresee the processes which will ensure the existence of another wasp next summer. In fishes and birds the most remarkable instincts are concerned with the perpetuation of the species by means whose operation the animals cannot foresee; and the same thing is true of mammalia. In some cases provision is instinctively made for unfore-

[1] I have to thank Dr C. S. Myers for some valuable suggestions in the course of this paper.

seen wants of the individual, as in the storing of food for winter by squirrels and some rats and by the curious bird *Colaptes mexicanus* (allied to the woodpecker), which lives on insects when he can get them, but stores acorns against the time when insects will be scarce. But the life of fishes, reptiles, birds and mammals, for most of the year, seems to depend upon getting food and shelter by a sort of haphazard intelligence. It is only when intelligence has been enriched by the growth of effective memory and accumulated experience that it can make any approach to the superseding of instinct by preparing for remote ends. Even then it may be said to be an extension of instinct; for, first, its effectiveness for conduct (apart from which it could never develop at all) depends upon the excitability of instinct by ideas (which intelligence presents) instead of by objects as in the lower animals; and, secondly, the wide adaptability of intelligence by acquired knowledge of the properties and relations of things depends upon the development of a special instinct of curiosity. Instinct is an organisation for the attainment of ends before there is a long enough chain-memory and knowledge of conditions to adjust means to ends according to experience.

The growth of intelligence in the higher mammalia, and especially in monkeys and man, depends, as W. McDougall observes (*B. Journ. of Psych.* Vol. III. No. 3), on a prolonged youth and parental care. We have seen that intelligence in one of its functions consists in trying one action or another and remembering the consequences—effectively remembering them, that is, in the sense that behaviour is modified for the future, though there may be no memory in the shape of "images." An animal will try more, the greater its activity and the greater its plasticity. Plasticity implies, first, an incomplete organisation such that, instead of fixed or nearly fixed reactions to an object, some variety of impulses is evoked; and, secondly, a more or less lasting modification of the organism by any impulse and its successful or unsuccessful result, without which there is no memory. The young of the higher mammalia are born in a state of helplessness; they present, as it were, a continuance of foetal conditions after birth, a generalised type of organisation to be completed by experience. Experience is to be gained by trying; but trying is dangerous; so that, in the first place, in order that they may try their powers with the least risk, they are soon ready to play; and their play is an anticipation of adult activities in an ineffective form (except for the sake of play); an anticipation which seems to resemble the shortening of phylogenetic processes that sometimes takes place in embryonic development. The ineffectiveness of play activities (except for play itself) depends partly on the immaturity of the organism, as in the courtship-play of some young animals; or, in other sports, on the feebleness of teeth, claws, etc., but chiefly on limitations involved in the utility of the activity, which would fail if play turned to fighting. It is needless to suppose with W. McDougall that this limitation depends on the impulse of rivalry (*Social Psych.* Chap. IV.). In the second place, young animals are protected from danger at play by parental care actuated by parental instincts. Thus in their plastic youth they learn by experience; and the fact of being born undeveloped makes the growth of definitely adapted chain-instincts impossible: the neural connections do not at first exist in the brain, and experience intervenes before they can be formed.

Amongst gregarious animals, parental care may be supported by the protection of the herd; and this seems to me to throw light upon the nature of the intelligence attributed to ants, sociable bees and termites. Taken singly, such animals do not display much intelligence; whilst the co-operative work of the hive or nest is amongst the greatest wonders of nature. This perhaps may be best explained by the incessant trying of all the operative ants, or bees, or termites at their several tasks, in which individuals often fail, but have their work made good by the trying of others. An instructive paper by Turner on "The Homing of Ants," in the *Journ. of Comp. Neurology and Psychology* (Sept. 1907), concluded that the instincts of ants are not definitely adjusted to special tasks, but "generalised": to go out foraging; to carry out of the nest dead or useless things; to bring home pupae, lost ants, food; and to do such things as best they can, not in uniform ways; and that the appearance of *concerted* division of labour amongst them is probably deceptive, and rather due to accidental coincidences; as when some ants hide pupae under a stone, knowing no better place to put them, and then others, who know the road home, carry them there. The success of such societies, then, is due to incessant free trying under conditions in which not much harm can be done by individuals, because their mistakes will be rectified by others so far as to maintain the life of the nest as a whole; each experiments under the protection of the rest, just as the young of the higher vertebrates experiment under the "protection" of the limitations of play and (more literally) of their parents. Against the great danger of dispersal in the course of independent trying, ants, bees, and termites are protected by the gregarious and homing instincts, chiefly controlled by the odours of the nest and of one another; and one may observe that their communities are rather families than societies. The most difficult thing to understand in these creatures is the plan of the dwellings of South African termites—if they are really always constructed in the elaborate way of those that I have seen described; for I cannot attribute the plan to a termitic "over-soul."

§ 4. As to the physiological correlative of instincts, considered as complex reactions of the whole organism to external conditions, if we consider only vertebrates, it seems to lie in the highest regions of the nervous system prior to the growth of the cerebral cortex. For Edinger has pointed out that the principal animal instincts, fear, anger, gregariousness, etc., are shown by fishes (*Journ. of Comp. Neur. and Psych.*, Vol. XVIII.); McDougall has shown that the emotions are phases of the manifestation of instincts; and F. W. Mott and Pagano have given reasons for thinking that the emotions and instincts are organised in the optic thalami and corpora striata. Goltz's dog, which had lost a large part of the basal ganglia, still showed anger, but no sign of pleasure, fear or affection. The cry of distress, which must be considered an instinct (being related to possible aid from others), though a very simple one, has been located in the posterior corpora quadrigemina. Lower still, in the medulla oblongata, come the centres for the compound reflexes of sneezing, coughing and sucking; whilst various reflexes more or less simple are co-ordinated through single segments or certain lengths of the cord.

All reflexes and instincts, so far as the striated muscles and the joints are concerned in their expression, are reflected in the kinaesthetic area of the cortex. Hence the outward expression of emotion is under the control of will; and this explains how an actor (according to Diderot, the highest kind of actor) can play a pathetic rôle without feeling it. The basal ganglia are not involved: nay, their action must be inhibited; else they would become active through their associations with the skeletal movements that normally accompany their action. The inhibition may be supposed to result from concentration of attention upon the details of minute expression. But whether the mimicry can be complete in tone, gesture and facies, without the primitive instinctive fervour, is questionable. However, the cortex, on the one hand, gives an immense extension to instinctive activities by awakening them in relation to remote objects[1], and later, through ideas, and by enabling

[1] Sherrington has shown the importance of the distance senses in developing the cortex, *The Integrative Action of the Nervous System*, Lect. IX.

a representation of the vast array of means that may be necessary to their satisfaction—as may be seen in the human development of acquisitiveness, constructiveness, curiosity. Indeed, it seems possible that in the cortex a higher order of quasi-instinctive motives may be organised, such as the passions of romantic love, of liberty, of justice. On the other hand, the cortex checks and qualifies the instincts by spreading the effect of whatever excites them through ideas of circumstances and consequences, which tend to excite other instincts and so to establish inhibition and deliberation. Deliberate action through means to ideal ends we call rational. As we watch a wasp eagerly digging a hole it knows not why, catching and burying a spider there with no further purpose, laying an egg upon the spider without any foresight of the consequences, covering up the hole as if that were an action for its own sake, we may call all this instinct, without a knowledge of the end. Making elaborate preparations for our own children whose birth is foreseen, then providing nurture, education, outfit, we have an end in view; but if any sceptic asks us why we pursue this end, we can give no more answer than the wasp. The end in nature, so to speak, is in both cases life, more life; and reason supersedes, or (rather) it partially enlightens instinct, because at the present stage of the world it generally ensures more life. But if here or there in the world the reproductive instinct fails us (as it does), intelligence cannot make good the deficiency.

II. The Nesting of Solitary Wasps.

§ 5. To illustrate the nature of instinct, I will take Solitary Wasps which have been so fully and delightfully described by Dr and Mrs Peckham[1]. Beginning with *Ammophila* as one of the best types, we find that she leaves her cocoon in the early summer, and spends two or three weeks flying about, feeding on flowers and mating, sleeping under the shelter of a leaf or in long grass. Then comes the time for laying her eggs. She first makes her nest in the ground slantwise, about an inch deep with a pocket at the end, and covers it up. Next she goes to find a caterpillar, seizes it, stings it in six or seven places, pinches the neck, and drags it off to her nest, which may be more than 100 feet distant. Arrived in the neighbourhood, she drops the caterpillar and opens her nest; then fetches the caterpillar, drags it into the

[1] *Wasps, Social and Solitary*. All page references with no mention of a book will be to this book. I have used it extensively, as the most trustworthy collection of observations known to me, and as the best proof of gratitude to the authors.

nest, lays her egg upon it about the middle of the side, and covers up the hole. She then makes another nest.

This is a typical case; but the nesting instinct is so far from being invariable that, though we may suppose all these solitary wasps to have begun in much the same way, each species now exhibits some modification of it. Thus some catch their prey before making a nest: others make a nest, and then hunt for prey. Some species build nests of mud; some use crannies in a wall to lay their eggs in, or holes in a tree, or the stalks of plants (boring through the pith), or the open ends of straws in a stack; some resort to human dwellings, chimneys, eaves, door posts. Some do not even make nests at all, but lay their eggs upon living caterpillars (*Microgaster nemorum*), or on chrysalises, the larvae pupating in the shell (*Ichneumon pisorius*). The gall-wasps are an allied family.

Different species attack different kinds of prey: flies (*Bembex*), beetles (*Cerceris*), bees (*Philanthus*), spiders (*Pompilus*); and, as a rule, each species confines itself to one kind of prey or to nearly allied kinds. Some species are content with one victim for their larva; others take two, and so on up to thirty or more. This depends partly upon the size of the prey—five large spiders may serve as well as ten small ones—partly upon the size the larva is to attain, or perhaps upon the nutrition obtainable from various kinds of prey. Whilst most solitary wasps stock their nest with food and then close it, *Lyroda subita* and *Bembex* feed their young from hour to hour until they reach the pupa stage.

Of species that burrow, some make a straight incline (*Ammophila*), some an incline leading to a level gallery (*Philanthus punctatus*); others a tortuous burrow (*Cerceris*). And some leave their burrows open until they are completely stocked, or even until the cocoon is spun (*Bembex*); others cover them up more or less every time they leave them.

Species also show various degrees of care in studying the position of their nests, flying about them more or fewer times before going hunting; and they have various degree of success in finding again their nest, or their prey, after leaving it.

Not only species but individuals of the same species show remarkable variations. In making their nests they bore to different depths, or in different materials; in covering up their prey, they display more or less care; in finding their way home, they are more or less skilful; in stinging their prey, they deliver more or fewer stabs, in different places, and sometimes kill, sometimes paralyse; in the number of victims the same wasp has been found to take for one cell of its nest fourteen, for another ten, for a third eight (*Trypoxylon rubrocinctum*) (p. 186).

No step of the nesting-instinct is infallible. Wasps of different species have been seen to begin to make several nests before succeeding. *Sphex ichneumonica* began, on stony ground, one nest, and gave it up, then tried another, finally completing a third (p. 56). *Aporus fasciatus* began and abandoned five nests, finishing the sixth. *Pompilus quinquenotatus* began eight nests before succeeding. Probably the reason for such failures is that the wasp comes upon a stone; for *Sphex ichneumonica* is said to have been working on stony ground; and in another case *Pompilus quinquenotatus* is said to have paused in the midst of digging, and then pulled out a pebble. Had the pebble been too large to pull out, she must have given up that spot. Wasps, then, have no infallible instinct where to dig.

Having prepared a nest and caught prey, they cannot always bring it home. Peckham saw *Amm. gracilis* carry a caterpillar for two hours a distance of 261 feet through all kinds of difficult ground, and then give up (p. 45). *Amm. vulgaris* was also seen to fail. Peckham says, "The affairs of Ammophila must often go wrong." *Pomp. scelestus* also failed to get home. Having brought their prey close to the nest, wasps cannot always find the hole. *Trypoxylon rubrocinctum*, building in a straw-stack, usually has to hunt about before recovering its nest (p. 186). *Pomp. fuscipennis* rarely circles about when leaving, and on returning hangs her spider in a crotch before opening her nest: she nearly always loses track of either the nest, or the spider or both (p. 221).

Having stored prey in the nest, a wasp sometimes forgets to seal it up. Of seventy-six nests examined, seven were prepared and sealed up empty (*Tryp. rubrocinctum*). The blue mud-dauber not infrequently makes the same mistake (p. 189). At every stage, therefore, the instinct is fallible.

§ 6. Intelligence assists this instinct in various ways. We do not see how else to explain the fact that burrows are shaped differently according to the nature of the soil; or that the same species will use a hole in a wall or post, or a straw, or a shell, as may be most convenient. The most undeniable proof of intelligence is given by their knowledge of locality, which is very variable, but nearly always wonderful. They gain this knowledge, no doubt, first of all, whilst flying about in the neighbourhood of their birthplace, before the time of nesting comes. But having made their nest, they fly about it in circles, making what seems to us a deliberate study of the locality, before going hunting; and if, having caught prey, they leave it for an interval to revisit their nest or what not, they sometimes study the locality before going away. Dr Peckham has given several diagrams of these studies.

This knowledge of locality used to be put down to a "sense of direction," or to a memory of all the turnings of a journey. It is also found in bees and ants and limpets and snails, in fish, birds and mammals, and probably in far more than have been observed. Some of the stories told about this faculty are certainly inexplicable, or perhaps incredible. But experimental evidence indicates that it is based on genuine memory and often, apparently, of definite objects. Avebury's experiments on ants, Fabre's and Romanes' on bees, and the Peckhams' on wasps, all go to prove this. The same explanation is given of the behaviour of carrier-pigeons. The Peckhams on three occasions caught some social wasps, the first that left the nests in the morning, and then stopped up the nest, and liberated the wasps a good way from home; the first lot from two positions a furlong out on a lake; the second within a barn, having windows at each end, one toward the nest, the other away from it; the third 300 yards away in the country. Of the whole, fifty to seventy per cent. returned to the nest. Of those liberated in the barn twenty-two, showing no sense of direction, flew toward the distal window, which was best illuminated; sixteen to the window in the direction of the hive. Peckham concludes that to find their way home they rose higher and higher in the air, flying in circles, until they saw some object they knew, and then made for it (p. 278). This is what carrier-pigeons do; but it implies a surprising keenness of vision in wasps.

At any rate, other experiments confirm the view that they identify a position by its relation to known objects. Bouvier cut away the plants around the nest of *B. labiatus*, and the wasp was confused, and spent a long time in finding the hole; he left a stone close to her nest for two days, then moved it 8 inches, and the wasp tried to find her nest under it as before (p. 124). Marchand observed *Bembex rostrata* leaving her nest on a stony hillside; he moved a swallow-wort that grew about 20 inches from the nest, and placed it 2 feet further off. *Bembex* returning flew to a spot in the same relation of distance and direction to the plant as her nest had formerly been, and could not find her nest. He then frightened her away and replaced the plant, and *Bembex* returning easily found her nest (p. 125). *Ammophila* deserted a nest in front of which some lines had been drawn in the dust.

But some indications of much higher intelligence than a knowledge of locality implies, are given by wasps in what Peckham calls their "use of the comparative faculty." He had several times seen wasps enlarge their holes when "a trial had demonstrated that the spider would not go in": and reports a case of this at page 303. Wasps have also been seen to bite off the legs or wings of victims too large for the nest. But once *P. scelestus* was seen to bring home a large spider, and on looking at her nest she "seemed to be struck with the thought that it was decidedly too small to hold the spider. Back she went for another survey of the bulky victim, measured it with her eye, without touching it, drew her conclusions and at once returned to the nest and began to make it larger" (p. 238). Such phrases as "measured with her eye," "drew her conclusions," may add too much to the observation; but reducing the observation to its lowest terms, it still seems to describe an act of comparison. Huber has recorded an observation on bees that has a similar implication (quoted by Houssaye: *Industries of Animals*, p. 241). One summer when the hives were much worried by unusual abundance of the death's-head moth (which will penetrate a hive to feast upon the honey), some bees blocked up the doorway of their hive, so that it was too small for the moths; but others built parallel walls of wax in front of the door-way, leaving between them a zig-zag passage too narrow for the moth to turn in; so that if he entered at one end of the parallels he had to go out at the other. Some bees, then, viewed the moth in breadth, others took his measure lengthwise. Less striking signs of a wasp's having some sense of quantity are shown by their supplying their grubs with approximately the same numbers of caterpillars, flies, etc.; whilst (as mentioned above) if the usual number is much departed from, it is when the victims in one set are decidedly larger than in the other, so that the amount of nutriment provided is about the same.

Something like intelligence appears also in the occasional abbreviation of a chain-instinct; as when *Sphex Ichneumonea*, which on bringing home a grasshopper, habitually leaves it a little distance from the nest, runs into the nest, returns for the prey and carries it to the edge of the nest, then goes in again and once more returning drags it in after her; yet when Peckham, whilst *Sphex* was in the nest the second time, removed the prey again and again, the wasp after the process had been repeated five or six times, at last dragged it straight into the nest (p. 304). Perhaps this is to be explained by fatigue; which often makes us when writing or talking drop syllables or words. An allied species observed by Fabre persevered, however, in following all the links of custom forty times.

The limitations of such intelligence as these wasps have are seen at every step. Although they remember the place of their nest, they may be unable to find the opening under the slightest concealment. *Aporus fasciatus* lost her nest when a leaf that covered it was broken off, but at once found it again when the leaf was replaced (p. 286). Loeb relates (*Comparative Physiology of the Brain*, p. 226), that *Ammophila* could find her nest in his garden, when unable to climb a wall that stood in the direct path, by going around through a neighbour's garden and through the fence, yet could not again find the opening of her nest when, in her absence he covered the hole with a clover blossom, though she found it as soon as the blossom was removed. Little intelligence seems to us to have been needed. Had she no experience of falling leaves and blossoms and of the changes thus made in the appearance of the ground? As to their powers of observation, why, on bringing prey to the nest do they so often enter themselves before interring the prey? We are apt to suppose that they go in to see that all is safe. But the most dangerous enemies may be there and yet pass unnoticed. In the nests of *Bembex* certain flies (*Miltogramma*) lay their eggs on the food provided by the wasp for her own young; yet when the parasitic grubs appear, she continues to feed them though her wasplings starve. Fabre, having seen a Sphex carry her prey into the nest, return and prepare to close it up, drove her away and took the prey, which had an egg attached to it; he then allowed her to return; when she went down into the empty cell, came up again, and stopped up the opening as if it had been "all safe" (quoted by Avebury: *Senses of Animals*, p. 253). Wasps that make their own nests rarely attack parasites, though they sometimes attack ants and other wasps that attempt robbery. If in some cases they drive away parasites, the rest of their conduct shows that this is not intelligent action: they do not know what the danger is. The whole family of *Chrysididae* seems to be parasitic upon burrowing wasps; yet no warfare is made upon them: the danger of their presence is not understood, and no effective defensive instinct has yet developed. The behaviour of *T. rubrocinctum* (p. 181) may be the beginning of such an instinct. Similar failures of intelligence were found by Fabre in mason-bees.

§ 7. In attempting to explain the origin and development of these nesting instincts in solitary wasps, I shall assume the general principles of Natural Selection; namely, that variations of behaviour that are advantageous to the species may be inherited, and accumulated by inheritance, and fixed: so that in course of time very complex activities may, through the survival of those individuals that inherit them, and the failure in competition of individuals less well-endowed, become characteristic of the species as a whole. How useful these nesting habits are is shown by an interesting fact. The species of solitary wasp keep up their numbers century after century, age after age, although each female wasp has (compared with most insects, most fish and even with many mammals) very few offspring—lays very few eggs—less than a score (as well as I can judge); and this suffices in spite of many parasites and other enemies. The fact illustrates the general rule of animated nature, that the greater the care taken of offspring, the fewer they are. It is an economy of physiological energy; and the rule is correlated with another rule, that the fewer the offspring, the higher is individual development; and every observer attests that the activity, adroitness and distinctness of character to be found among these wasps are astonishing. The rule is further illustrated in the case of *Bembex spinolae,* who, instead of storing her nest once for all with flies, laying her egg, closing the nest, and leaving it, attends to her offspring after it is hatched, and feeds it day by day until it reaches the pupa stage. She does this for one larva at a time, and each takes a fortnight, so that she cannot have more than five or six offspring in a season. Her method has a certain disadvantage; it gives more opportunities to *Miltogramma* to invade the nest, in which she is very successful. Peckham opened ten or twelve nests; only one was free from parasites: the others contained from two to five maggots of *Miltogramma*; yet *Bembex* flourishes. *Lyroda subita* likewise feeds her young from hour to hour, but I do not know that the number of her offspring has been observed or calculated.

But this nesting instinct is a chain-instinct, a series of totally different actions, and to explain it we must consider each step, and also the order in which the steps occur. In the first place, then, we observe that (1) to hide an egg in a hole or other shelter is plainly useful; (2) so it is to hide or cover up the opening of the hole; (3) to lay food by the side of the egg, or the egg by the side of the food, is useful even if there is no nest; (4) to bring more food is useful, if it enables the larva to attain a better growth, or development or potentiality, before the pupa stage; (5) to kill living food, or paralyse it, is useful that it may not injure the egg or young larva; (6) to inspect the nest from time to time is useful, in spite of actual shortcomings;

(7) to explore the neighbourhood and to identify the spot are useful actions, if the egg and larva are afterwards to be provided for; (8) to return (or "home") is useful.

Such actions, being useful and immediately useful, will, if they occur in any individual, be perpetuated and tend to become specific: but, in the second place, how do they occur? Let us begin with the making of the nest. To dig a hole in the ground, or in the stump of a tree, or in the stalk of a shrub, or to build a mud cell, as some wasps and some bees do, without knowing what is to be done with it (for plainly they cannot know)—is not this an extraordinary operation? To understand it we must show how it may arise from simpler actions more commonly performed by animals, especially by insects, if possible by hymenoptera, and particularly wasps. We may assume that the peculiar actions characteristic of species of wasps, have been differentiated from a common ground. To find a shelter of some kind for itself or its progeny is an action common to most kinds of the higher animals and to very many insects. Amongst wasps it sometimes takes the form of creeping into a crack in a cliff, or wall (since walls have come into existence), or into a hole in a tree, whether the crack or hole has been made by the ordinary wear and tear of nature, or by some other animal. Whereas Peckham observed that the *Pompilidae* near Milwaukee dig their own nests, Fabre reports that in France the *Pompilidae* do not make their own nests, but lay their eggs in crevices, selecting a suitable crevice before catching their prey (p. 197). Near Milwaukee *Odynerus capra* has this habit (p. 94). The utilisation of a crevice in a wall, or a hole in a tree, already existing, I take to be the beginning of both masonry and pit-digging. *Trypoxylon rubrocinctum* (which preys on small spiders) was found by Peckham to be nesting in the cracks of a brick wall; but as the cracks were too deep for their purpose, the wasps "built a mud partition across the opening about an inch from the outside of the wall" (p. 178). This must be a useful protection against possible enemies on the other side. Wasps that nest in the hollow stems of plants act similarly, making partitions at such depths as suit their purpose. Slight variations of this practice in a wider crack would result in building a mud-partition all round; and that is to make a cell. Having made a complete cell in a crevice, it might be made in the hang of a cliff or on the bough of a tree, if there was anything to gain by it. On the other hand, suppose the natural crevice to be too small, then to kick out loose grains of earth or rubbish—or at a further stage, to bite away some of the wall, or the wood of a tree—would be a useful practice, and if inherited would be an occasion of selection. But this is nothing else than to dig. Another slight variation would transfer the work to the ground: first using holes already existing, then enlarging them, then digging fresh ones. *Cerceris deserta* was traced by Peckham to its nest in a crevice amongst some lumps of earth (p. 152); *Pomp. marginatus* was traced to a crevice amongst some lumps of earth where she was making further excavations (p. 229). Nests vary in depth from 1 inch (*Trypoxylon*) to 22 inches (*Phil. punctatus*). Few wasps can have such an opportunity of economising labour as that which is taken advantage of by one described by Hudson (*Naturalist in La Plata*, p. 181). This wasp preys on a spider, whose habit is to lurk in ambush in a hole whence it rushes out to seize any passing practicable insect. The wasp tempts this spider out, kills it, lays an egg upon it, and buries it in its own den.

In this instinct then we find every stage of development still represented by the habits of extant species, from the use of a crack to the making of a burrow 22 inches long. Let us next consider a certain variation of this instinct in relation to the taking of prey. Whilst *Ammophila, Cerceris, Sphex, Ichneumonea* and most solitary wasps make their nests first before taking prey, there are some—five species of *Pompilidae* observed by Peckham, *Aporus fasciatus* and others—that first catch their prey and then construct their nest. The latter course has certain disadvantages; for whilst the nest is being dug, the prey is liable to be carried off by ants, or by robber wasps, or to be attacked by parasites; and to guard against this the wasp frequently leaves off digging, to see that her prey is safe. Fabre thought that one Sphex that dug her nest in the neighbourhood of prey already captured, did so because the prey was too large or heavy to be carried far. But the practice seems not to be confined to wasps that take heavy prey; it does not hold with many that do take heavy prey (*Ammophila*); and Peckham saw *Aporus fasciatus* drag for some distance a spider much larger than herself, and deposit it on a melon leaf whilst she dug a nest (p. 81). The danger of leaving the prey whilst making a nest is sometimes partly avoided by *Pomp. quinquenostatus* in a remarkable way. Instead of leaving it on the ground, she hangs it in the crotch of some plant-stem; but even then it is not safe from robbers. This device, however, is not constantly followed: the wasp sometimes leaves her prey on the bare ground.

It has often been objected to the theory of evolution that we never see any species in process of changing form or colour; and the same objection might be urged against the evolution of instincts. It depends on an illusion similar to that implied in the term "fixed-stars": we cannot see the stars move, but we can calculate the direction and velocity of the movement of very many of them from facts that can be seen. So no doubt species and their instincts are always changing, but much too slowly for us to notice it within the limits of our short lives. We can, however, sometimes find in natural history, without appealing to embryology, evidence of the changes that have probably been undergone, and may sometimes find a condition of things that seems to imply that a change is now in progress. In such a condition perhaps are these instincts I have just described. When a wasp catches its prey before digging a nest, the simplest supposition is that, at first, the prey was left meanwhile upon the ground. It was an improvement upon this when prey was first hung upon a plant until its grave was ready, but not so great an improvement as quickly to exterminate the other practice; and so we still see them existing side by side in the life of the same species. Naturalists who live 50,000 years hence may find that the more careless practice has been entirely lost, or only occurs by atavism in idiot-wasps. But, further, the whole double process of either capture and digging, or digging and capture, may be in a state of change: the latter seems to be the commoner; and since it gives greater safety and economises time and energy, it may be gradually exterminating the former course.

To understand the matter we must try to find how both processes arose. To begin with the case in which capture precedes digging. The capture and killing, or paralysing, of prey in order to lay an egg upon it, is itself a complex process, which must have had a history. We know two simple cases: first, the depositing of eggs upon animals already dead, as by the Blow-fly (*Calliphora erythrocephala*), and by carrion-beetles (*Necrophorus*), and by parasitic wasps (*Cerophales* and *Pomp. subviolaceus*); and, secondly, the depositing of eggs upon living prey. The latter course is adopted by many flies; and amongst wasps by various species of *Ichneumonidae*, which lay their eggs upon living caterpillars on whose juices the larvae feed, and by some *Braconidae*, a closely allied family; and *Pompilus trivialis* oviposits on living spiders. Since a living caterpillar upon which an egg has been laid is still exposed to the attacks of other parasites and enemies, it may give greater safety to kill it; and this is shown to be probable by the comparatively great number of eggs deposited by *Ichneumonidae* and *Microgaster*. But much greater safety is obtained if the prey is not only killed but also hidden in a hole or cell. *Necrophorus* buries the carrion on which its eggs are laid; and parasitic wasps lay eggs on victims already hidden, or about to be hidden, by other wasps. With one utility depending on another, the combination of killing or paralysing the prey with the hiding of it is not more improbable than the combination (say) of imitative colouration with imitative flight in some butterflies.

If prey, killed or paralysed, is to be hidden, there are two ways of doing it: (1) by finding then, for the first time, a suitable hole, or by enlarging one, or by digging one; (2) by carrying it to a hole or cell already known or prepared. The former course may seem the simpler, involving the less imitation of foresight: in a wasp (we may say) flying about in summer weather, the need to oviposit matures; this excites the impulse to catch and kill a certain bee, and then comes the impulse to hide it and, therefore, to search for or dig a nest. But this only seems the simpler course if we suppose the wasp not yet acquainted with any suitable hiding-place. In many cases, however, they may have, or may anciently have had, a place ready, namely, their sleeping place; or the cell from which they themselves emerged, which may also have been their sleeping place. At present some wasps (including males) dig holes to sleep in; some "congregate at night in convenient crevices"; some, after the nest for their eggs has been made, sleep in it themselves (p. 117). Others sleep under leaves, or in long grass. Perhaps these last show the greatest deviation from original habit.

Peckham gives this very curious account of *Philanthus punctatus*. Her nest is a long gallery with pockets, in each of which an egg is laid with food for the larva. When the wasps emerge from their cocoons they live together for a time in the parent nest, flying abroad by day and returning to it at night. Such a family was found to consist of four females and three males. One of the females, the first maturing, enlarged the old nest for her own eggs; the second, a day later, left the nest, and made a new one close by; five days later, a third female, having already left the first nest and lived for two days in the second, made another for herself. The three males still lived on in the old nest with two females, one of which (as far as observation went) remained barren. One at least of the females that matured later than the first was seen to work at the old nest along with her sister, the new owner; and all, including the males, seemed to keep guard over it. Here, then, in the case of the first maturing female, there is a plain example of a wasp that before killing its prey (*Hallictus*), has a nest ready; and to bring the bee to it is merely the homing instinct that is found in animals of all orders. If few wasps are known to use their old nests, it may be that the practice is insanitary, and so has been generally eliminated. And for an earlier breaking up of the family (which is usual) than occurs in this case of *Phil. punctatus* there is a good cause, namely, the advantage of cross fertilisation.

The second female to mature made a new nest; and, at first glance, this seems to be an original action; but it is not. For the first one enlarged the old nest; and to make a new nest from some neighbouring crack or hole in the ground, is only to do the same thing a little more thoroughly. We can, however, see the opportunity for a different order of actions to arise at this point. Suppose the second female to begin, like the first one, by catching a bee, and to return with it to the old nest, and to be driven away. She must then make a new nest after catching the bee, or else her offspring perishes. If, however, she does make a new nest, and her offspring survives, and inherits this variation of first taking prey and then digging its grave, the species in each generation will consist more and more of wasps that follow this practice; since the offspring of the first maturing female will be fewer than those of the more numerous later maturing ones; and in some species this practice has become the rule.

Before leaving this case of *Philanthus punctatus*, I will venture to suggest that it points to a possible origin of sociality in wasps, bees, ants. Several species of wasps are semi-social in the sense of making their nests near together: *Bembex*, for example; but these are apt to quarrel and rob one another; there is no co-operation. Wherever we find true co-operation amongst these Orders there is "caste" or dimorphism. Now if the fourth female of *Phil. punctatus* that was not seen to leave the nest, was actually barren, and if she assisted at clearing out the old nest, as one of the sisters of the owner was seen to do, we have here the beginning of a composite nest. It was already strong in drones. That a barren female may become a worker, it is a necessary variation that the impulse to work at the nest should be stimulated by something else than the need to oviposit—say by the sight or smell of the nest, or of another at work. The only other approach to co-operation observed by Peckham was made by *T. rubrocinctum*: the male sat in the opening of the nest and drove away intruders during the absence of the female; and, on her return, made way for her, and sometimes carried in and stored the prey, whilst she flew away for more (pp. 181–2).

§ 8. To return to the nesting instinct: why do wasps seek any shelter for their eggs; why construct cells, or creep into holes or crannies? Do they foresee that their progeny have enemies; do they understand danger and safety? We cannot suppose so much. Probably to explain this matter we must fall back upon primitive tropisms—phototropism, or thermotropism or stereotropism. These impulses in such highly evolved creatures as the wasps, may date from remote ancestors in an age before our wasps had become wasps, and may remain active in existing species under conditions in which they are still useful and so far as they are useful. Wasps love sunshine and warmth; shun cold and wet; as the shadows of the afternoon lengthen, nearly all of them seek some sort of shelter, some being content with leaves or grass, others requiring more substantial protection. Peckham indeed mentions (p. 108) one species, *Crabro stirpicola*, that worked through the night at excavating its nest in the stem of a plant; but as it was under the shelter of a glass bottle provided by the naturalist, the bearing of the observation is a little doubtful. How little the seeking of shelter upon the impulse of a tropism implies any idea of danger, is shown by Loeb's amusing observation upon a butterfly, *Amphipyra*. Placed in a box, half of which was darkened and afforded concealment, whilst the bottom of it elsewhere was strewn with small glass plates, raised upon blocks just enough to allow the insects to creep under them, some specimens of this butterfly "collected under the little glass plates, where their bodies were in contact with solid bodies on every side, not in the dark corner where they would have been concealed from their enemies" (*Comparative Physiology, etc.*, p. 184). They did this both in direct sunlight and when the whole box was darkened. Hence stereotropism which normally gives concealment, remains compulsive when it gives no concealment. If, then, the nesting instinct of wasps be traceable to a tropism, we need not suppose that it implies any idea of the safety of the egg or larva.

But granting an original tropism as the basis of nest-making, we are still required to explain why at a certain time the behaviour originally determined by this tropism becomes effective, contrary to the animal's usual habits, in the morning or middle of the day, so that it suddenly begins to burrow in the ground or to wall up a cranny.

This is an example of a great class of problems presented by the existence of critical points in the life-history of animals. Why do birds in autumn feel the impulse to migrate, in spring to build nests; why does a caterpillar at a certain time begin to spin its cocoon, knowing nothing of the pupa stage upon which it is about to enter? And so on. Such changes seem to depend (*a*) on external conditions of temperature, food-supply, etc.; (*b*) on internal conditions, a certain maturing or modification of the organism, producing perhaps an uneasiness that is relieved by a certain action. In wasps the approach of the time for laying an egg brings on a complete change of behaviour, so that instead of sporting about amongst the flowers, paying no attention to insects or animals of any other species, she begins to burrow, or to catch bees or spiders. By merely natural-history methods we cannot explain this: it is intrinsically a physiological question. But perhaps Psychology will help us to something better than mere blank astonishment.

We observe, then, in the first place, that, when the impulse to make a nest is felt, there seems to be a sudden narrowing of consciousness, such as occurs in ourselves in the attitude of close attention; so that the wasp becomes interested only in a certain feature of the ground, or of a tree stump—if preparation of the nest be the first link in its chain-instinct. Conceivably, such a restriction might begin in the receptor-organs, their range being limited to the important object, so that the wasp can see nothing but that feature of the ground or tree. But more probably, it is due to the opening of an internal door that gives a certain perception access to the sources of certain motor activities. The sense of hearing seems to be strangely specialised in some animals: Edinger says (*op. cit.*) that a lizard may give no reaction to the most violent noises, such as loud singing, or banging a stone, and yet be at once on the alert at a slight rustling in the grass; there is mutual recognition of calls between lamb and dam; bees seem deaf to most sounds, but are said to be immediately affected by a peculiar cry of their queen; Peckham reports that social wasps took no notice of various noises he made, but seem to be affected by their own buzzing (p. 9); and elsewhere he speaks of *Clorion* as apparently listening to a cricket and being guided to its capture by the noise (p. 256). It is difficult to understand how in any of these cases the range of a sense-organ can be restricted to one sort of object. A more reasonable supposition is that the conditions of reaction are central; that in the case of wasps that begin to burrow, the internal maturing of the organism accompanying the development of eggs, releases an impulse when the ground, tree-stump, or whatnot is seen; that, in fact, such an object then for the first time becomes interesting in a peculiar way. This is analogous to the interests that from time to time possess ourselves, especially during childhood, and often predominate for a time almost to the neglect of everything else: such as babbling, running, climbing, stone-throwing, collecting. The wasp also seems suddenly to have no regard for anything but digging or plastering. And in her unconsciousness of purpose there is a further analogy to the play of children; for this we know has, *in ordine ad universum*, the great utility of developing their powers of perception, activity, imagination; but they think no more of that than the wasp does of the egg she is about to lay or of the imago that will sport in the sunshine next summer. Indeed the absolute detachment of play-interest, absorbed in itself, seems to be a survival of the original instinctive form of all activity, undisturbed by intelligent appreciation of further ends.

This interest lasts until a certain result is attained, and the wasp is then diverted by another critical change to another activity. The attainment of the result of digging or plastering cannot be measured by the time taken or the energy expended; for observations show that these vary greatly; and, yet, can it be the *form* of the work, that satisfies her, as it does an artist? The nest completed, the wasp hides it, or not; flies about to study the locality, or not; then whirls away, hunting it knows not what; and presently the sight of a bee or spider, its special prey, excites a new interest and a new impulse. Again it attends to that only. The victim is seized and stung; and then the homing impulse awakens; and so on until the whole task is finished.

§ 9. The remaining links of the chain-instinct are much easier to understand. Take first the amount of food supplied to the larva. Whilst *Ammophila*, capturing good-sized caterpillars, can sufficiently provision her nest with one of them, other wasps, capturing smaller prey, bees or flies, provision their nest with many victims, half a dozen, a dozen or more. Such a number is necessary for the development of the normal imago. For every species of animal there is, in a given environment, a certain normal stature, which few fail to approach and few exceed. In insects that undergo metamorphosis, the size of the imago depends upon the nutrition of the larva. If, then, we suppose a certain species of wasp to vary in such a way that, instead of taking large prey, one of which would suffice, it turns to smaller prey, it must also vary in the direction of supplying its larva with more victims, or else the species must dwindle proportionally in magnitude, or even perish. And a change of size must often lead to extinction, unless accompanied by further changes of habit.

We are thus led to a very interesting question—why does each genus or species of wasp confine itself (with few exceptions) to one kind of prey, or to closely allied kinds? Addiction to one kind of food is very common in the animal kingdom, and amongst insects: lepidoptera lay their eggs, species by species, each upon one kind of plant; gall-wasps frequent the same trees or shrubs. Some advantage is implied in this, in spite of the disadvantage that the flourishing of each kind of plant varies from year to year, and that therefore the food-supply is sometimes relatively scarce. The same thing is true of animal prey. As to wasps each kind of prey must be hunted in its own habitat, must be seized in the most advantageous way, must be stung in the most advantageous way, must be stored in the most advantageous numbers; and it plainly needs a much simpler adjustment to deal in the most advantageous way with one (or with closely allied) species of prey than with many different ones. It is the utility of all specialisation to do one thing well. There is physiological economy, and it is marked by anatomical adaptation—very apparent, for example, in *Ammophila*.

The killing or paralysing of prey is a very variable action. *Ammophila's* caterpillars are sometimes killed, sometimes paralysed; and it makes no difference to the grub whether its food be dead or alive. Some flies stored by *Crabro* were so slightly injured that they flew away when the nest was opened (p. 101). Energetic movements of wounded prey are dangerous to the egg, as seems to be shown by the practice of some wasps of suspending their egg by a thread from the roof; yet *Aporus fasciatus*, taking spiders, probably "depends upon packing her victims in tightly in order to keep them quiet" (p. 83). *Tachytes* is the most perfect paralyser of all; but so short a time elapses between the laying of the egg and the spinning of the cocoon, that its adroitness is of no use to it (p. 252). How shall we explain all this? By economy. To paralyse or to kill is indifferent; but poison is a physiological expense; and the tendency is to administer no more than will just serve the purpose. What may be the feelings of the wounded victims we can but faintly surmise: in the arrangements of nature they seem not to have been much considered.

The repeated exploring of the nest by some wasps seems a useless action, when we find that, after all, they do not notice the presence of parasitic eggs, nor even the absence of their own eggs. It is clear that they have no idea of the dangers that beset them, nor of the biological purpose of their actions. Perhaps the sole use of exploration is to provide that the nest, as a nest, shall be intact and adequate, that it shall be large enough, and that the roof shall not have fallen in.

The use of covering the nest and concealing it, though comparatively neglected by some wasps (*Bembex*), and only partially performed by others (*A. polita*), seems pretty plainly to consist in the exclusion of parasitic flies and wasps; which, if they get the chance, enter nests and leave their own eggs there. In one species, at least (*Aporus fasciatus*), this practice of covering the nest has become so fixed, that if they begin a nest and find the place unsuitable, they fill in the hole before beginning another (p. 82). It is done, therefore, without conscious purpose, yet sometimes with extraordinary perfection: as by *P. fuscipennis* (p. 218) that was seen to pound the earth over the mouth of her nest with her abdomen, sweep it smooth with her legs, and finally bring small objects to conceal it—"a little stick, the petal of a faded flower, a scrap of dead leaf, and so on until 10 or 12 things had been collected." Surely a work of supererogation, which no other wasp of the species was seen to emulate. *Ammophila* is sometimes careless but usually very careful in closing her nest.

The most unsatisfactory part of the wasps' nesting instincts appears in their behaviour to parasites. They sometimes drive them off in a feeble manner, or try to avoid them, but have never (I believe) been observed to attack and kill them; it is as if they regarded the parasites as annoying but not dangerous. Their behaviour to ants is very different. One wasp (*Pomp. scelestus*) was seen to try to kill an ant by seizing it furiously and throwing it back against its sting (p. 238): others (e.g. *Pomp. fuscipennis*), on the approach of ants, "make off with every sign of terror" (p. 219). Yet *Aphilanthops* preys upon winged queen ants, and *Fortonius* upon workers. Probably the relations of wasps to ants are more ancient than to any sort of parasite, and therefore the adaptation to them is more complete. We may assume that parasitic wasps once had the same habits as the rest, and that their degeneration is comparatively recent. In relation to parasites, then, the instincts of wasps are still in course of development. And plainly, considering the matter psychologically, the narrowness and intensity of any instinctive interest are opposed to variations enabling them to deal effectively with new conditions: it is the opposition of organisation to plasticity.

If it seems difficult to develop such chain-instincts as these wasps display by natural selection of occasional small variations, or even of considerable variations, such as the bringing of a second or third fly or bee, there has been plenty of time to do it in. Hymenoptera are found throughout the Tertiary strata, perhaps even in the middle of the Secondary (Jurassic)—a good many million years ago. Similar species of wasps and ants with similar habits are found in North America and in Europe, and must be supposed to have spread when the Arctic regions were viable; for so many resemblances can hardly be accounted for by such methods of migration as the occasional transportation of colonists by floating timber.

§ 10. The Intelligence shown by solitary wasps may be considered under three heads:

(1) The nature of their Memory, which is conspicuous in relation to locality. Locality-memory is widely distributed throughout the animal kingdom. A horse often travelling the same road comes to know (I am told) every object by the wayside, and is uneasy if anything is added or taken away. Snails, far removed from both horses and wasps, know the way back to their shelters. So do limpets to their old scars. Lloyd Morgan (*Animal Behaviour*, p. 156), experimenting upon limpets, found that of twenty-one moved a distance of 18 inches, eighteen (nearly ninety per cent.) found their way back; of thirty-six moved 24 inches, five (about fourteen per cent.) got back. Amongst Hymenoptera, ants find their way for considerable distances, guided apparently by the direction of light and by odours. Knowledge of locality is very important to animals, especially to all that have homes. Some migrating birds are said to return year by year to their old nesting haunts. The carrier-pigeon is notorious. No animals need it more than these wasps.

Amongst mankind, savages acquire a minute knowledge of locality, sometimes over wide areas. To townsmen exact knowledge of locality is so unimportant that they have difficulty in understanding how it can be acquired. We attend to and remember, at most, conspicuous landmarks and general directions. Usually in going about we think of something else. If we notice particular objects, it is not in their place relations, but as of this or that class, or as presenting some unusual feature; and they start in us trains of thought.

It may help us to understand the memory of wasps and bees if we consider that the context of place is all-important to them; that they live on the perceptual plane, and are not distracted by concepts or trains of thought. Hence it is almost or quite impossible for us to see a group of objects as they see it. Perception is only the starting point of our knowledge; for them it is all in all. To appreciate the difficulties that beset a homing wasp, we must remember, that whilst some species seek their prey on the wing and fly home with it, others that seek their prey on the wing take victims of such a size that they are obliged to drag them home along the ground, perhaps through stubble or brushwood. In the latter case they cannot see their way beyond a few inches, and all their landmarks are hidden. Then Peckham reports several cases in which the wasps leave their prey from time to time and return for it. We may surmise that the intervals are spent in flying up into the air to locate known objects, or in actually revisiting their nests: in either way reascertaining the direction. And whilst dragging their victims along through stubble they may find their way less effectively by the direction of the light. If the journey takes a good while, as it sometimes does, the direction of the light becomes misleading. They do not always get home. In fact in this way those wasps that make their nests first, and then go hunting far afield, are at a disadvantage compared with those that first catch their prey and then make a nest near at hand. The former need greater powers of observation and memory.

But further although several wasps before leaving the nest fly in circles and seem to study the spot, yet these circles of direct study do not seem to be very wide. They then fly to a distance from which the near neighbourhood of the nest may be hidden: in returning they must trust at first to other landmarks. But how difficult it is to recognise an object—say a tree, that has not been specially circled—from a new point of view. It seems to imply the sufficiency of very partial and something like analogical recognition, and without ideas. In ourselves it is plain that recognition does not always involve ideas, may depend upon features that cannot be precisely indicated, and indeed primarily consists (as it seems to me) in exciting a certain mode of reaction. In wasps, it determines them to fly in a certain direction. This may be the essential character of their memory. Further investigation is needed as to the areas within which their recognition of locality is effective, and as to their means of orientation, whether by the direction of the light or what else, when beyond those areas. Guidance by the direction of the light may be connected with their preference for working in clear weather.

(2) Their behaviour in respect of quantity and form. Each

burrowing species (and these remarks apply equally to the masons) has its own customs of always making a nest nearly the same size, of nearly the same depth, sunk nearly in the same direction, with one or more pockets, and of storing it with nearly the same amount of food. Its first nest is made by each individual nearly according to type. What determines such uniformity of behaviour? If it were merely a question of the amount of excavation accomplished, we might suppose that the critical change that releases the burrowing impulse also supplied energy for just so much work. But this is incompatible with the fact that wasps often begin one, two or more nests and abandon them, and yet complete a nest at last. They have therefore more than enough energy for one nest. But at any rate a definite supply of energy would not explain the nearly uniform shape, and pocketing of the nest. Can they have observed the shape of the nest from which they themselves emerged? This seems very unlikely; and the parallel explanation of the specific architecture of birds' nests has been refuted by the observation that birds bred in a felt nest will nevertheless next year build according to the ancestral pattern if they get the materials. Each wasp works alone: we cannot see any explanation analogous to that which Darwin gave of the cells of the hive-bee. And I cannot perceive any correlation between the shape and structure of a wasp and the form and direction of its burrow. We may suppose a certain satisfaction when the work is done, but what is the ground of the satisfaction?

Similarly as to the amount of food stored, in each case it seems to be about enough. And the size of the prey brought home is usually such that it can be carried into the nest: *T. rubrocinctum*, says Peckham, never takes too large a spider for the calibre of the straw in which its nest is made (p. 184). This indeed may be understood as a necessary mutual adaptation between the size of the nest made or selected, and the size of the prey that excites the impulse to attack. But with some species the prey brought home is not infrequently too large for the nest. In one case already mentioned, Peckham thought that this situation incited the wasp to a definite act of comparison. Was it the first time that that wasp had met with the same difficulty? If not, its behaviour may have been due to the effects of former experience. But we had better not theorise on such a unique observation. Generally, when a wasp brings home prey, it first tries to pull or push it into the nest; if it will not go in one way, it tries another; or it bites off legs or wings to reduce the size; or it enlarges the nest.

There are these three courses open to it, and it may try them all; an admirable proof of the plasticity of its organisation, but not requiring ideas or anything else beyond the impulse to get the prey in, which is the instinct itself. Perhaps the wasp does not display greater resource than Darwin reports of earthworms when dragging leaves into their burrows (*Vegetable Mould,* etc. Chap. II.). Upon this he comments as follows: "If worms acted solely through instinct or an unvarying inherited impulse, they would draw all kinds of leaves into their burrows in the same manner. If they have no such definite instinct, we might expect that chance would determine whether the tip, base or middle was seized. If both these alternatives are excluded [as he had already shown], intelligence alone is left; unless the worm in each case first tries many different methods, and follows that alone which proves possible or the most easy; but to act in this manner and to try different methods makes a near approach to intelligence." We may say the same of wasps. Trying is not intelligence, for this implies at least a scintilla of foresight; but it is the necessary preparation for intelligence.

(3) The adaptation of means to ends. Anything in the nesting of wasps that looks like intelligence under this relation must be confined in each case to single links of the chain of activities. The chain is complete from the first; but the first time it is run through, a wasp cannot possibly foresee the next link, still less the final purpose or use in nature. Each instinctive activity contains its own purpose as an activity. The above cases of dealing with prey too large for the nest are a good example of this: the activity itself includes the end of getting a spider, or what not, into the nest; and for this they discover means by trying different courses.

Another case that excites admiration is the way in which *Ammophila* stings her caterpillars just between the segments where the ganglia lie, so as to obtain the greatest effect with least expenditure. She cannot possibly understand the anatomy of caterpillars. If we look at the illustration of this action given by Peckham (p. 27), we see the wasp with long legs, bestraddling the caterpillar, holding it fast by gripping the back with its mandibles, and tucking its long abdomen under the caterpillar so as to reach the ventral chain of ganglia. If this is the way in which Ammophila always stings caterpillars, its whole structure is adapted to such a method. But how does it find the position of a ganglion? A good many caterpillars (of which the one in the illustration is an example) have their segments plainly marked by external constrictions of the skin. Bestraddling such a caterpillar and drawing the tip of its abdomen along the side, it must catch in a fold of the skin, and that may (by a reflex) discharge the stab of the sting. In other caterpillars, however, the skin hangs loose, and would give no guidance to the stinging operation. Does *Ammophila* ever take such caterpillars; and, if so, does she find the ganglia with any precision? That she may act in the way I have described may seem probable when we consider the following observation of Fabre's (quoted by Houssaye: *Industries of Animals*, Chap. v.). Once when *Sphex flavipennis* brought a paralysed cricket to her nest, whilst she as usual entered the nest before dragging in her prey, he took it away and substituted a live cricket, hoping to see her method of attack; and in this he was not disappointed. After a struggle the cricket was turned on its back. Sphex seized with her jaws the end of the cricket's abdomen, placing her legs on its belly and with her two hind-legs holding its head turned back so as to stretch the underside of its neck. "The cricket is unable to move, and the conqueror's sting *wanders over the horny carapace* seeking a joint, feeling for a soft place in which it can enter to give the finishing stroke. The dart at last reaches, between the head and the neck, the spot where the hard portions articulate, leaving between them a space without covering, etc." The words I have italicised express the analogy to what is suggested above as the possible action of *Ammophila*. Not knowing *S. flavipennis*, I cannot judge whether her figure is specially adapted to her dealings with the cricket: it may be worth the observing.

Again, some wasps, as we have seen, catch their prey before making a nest; and whilst burrowing some of them leave their prey on the ground, some lay it on a leaf, some hang it in the crotch of a branching shrub. The last plan strikes us as a remarkable refinement upon the second, which itself seems to be an intelligent means to the end of putting prey out of the way of ants. But, really, the prey must be put somewhere; and these are almost the only places in which it can be put. Is it necessary to see more in such behaviour than three variations of placing the prey, none of which hitherto has had sufficient survival value to extinguish the others?

Take, finally, the case of covering up the nest whose use, unknown to the wasp, is protection against ants and parasites. We have seen that this is done with all degrees of care. Peckham reports (p. 38) an interesting observation upon *A. urnaria*: one individual of this species was seen to finish the closing of her nest by picking up a small pebble in her mandibles and using it as a mallet to harden and smooth the surface. He quotes W. S. Williston as having observed the same action as specific (apparently) in *A. yarrowii Cres.* If the action is specific, it is less probable that it is intelligent. We must consider that these wasps are accustomed to pull pebbles out of holes and to carry them in their mandibles, and also that they are accustomed to smooth the earth by striking with their abdomens and butting with their heads; and now some have taken to using pebbles instead of their bodies. This is all the variation; and what most puzzles me is that it should be useful enough to become specific; but there are numerous cases in nature in which the development of structure and function seem to have been carried to an unnecessary pitch of perfection, and for which nevertheless we can at present assign no other cause than natural selection.

The methods of Natural History and Psychology can only make a first approximation to the explaining of tropism, instinct and intelligence. Movements of pursuit and avoidance, plasticity, critical changes in the life-history of an animal or plant, original tryings, analogical recognition, memory, must all have grounds in the intimate constitution of living things: there must be a *latens schematismus* and a *latens processus* of these things, that for the most part remain to be explored and promise a boundless field for experimental industry.